THE SPERMATOGENESIS OF THE SPIDER.

WITH PLATES IX. AND X.

LOUISE BAIRD WALLACE.

About four years ago, when the present work was undertaken, several investigators had described a peculiar chromosome in insect spermatogenesis, but outside of the insects it had not then been reported and it was a matter of considerable interest to discover whether or not it obtained generally in the maturation of the germ cells of the Arthropoda. Since Dr. Montgomery had failed to find it in *Peripatus*, he suggested to me the advisability of trying some higher form. A study of the reproductive organs of *Limulus* was first attempted but these proved unfavorable on account of the minuteness of the cells. The testes of the spider were then examined and were found to be promising material for, as an offset to the rather large number of chromosomes characteristic of the Arachnida, the germ cells are of fairly good size and the peculiar chromosome forms a conspicuous structure of the cell even to a casual observer.

For various reasons the common tube-weaving spider, *Agalena nævia*, has been taken as the basis for work, but a comparative study of a few representatives from the Drassidæ, Attidæ, Lycosidæ, Theridiidæ and Epeiridæ was found of great value in the interpretation of some points. After the publication of a brief preliminary in the fall of 1900, the problem was laid aside until the fall of 1903, when it was resumed at the University of Pennsylvania uuder the direction of Dr. E. G. Conklin. It gives me pleasure to cordially express my indebtedness to Dr. Conklin for his ever ready encouragement and helpful criticism throughout the year.

METHOD.

By almost common consent the strong solutions of Flemming's chromo-aceto-osmic mixture and Hermann's platino-aceto-osmic mixture have been chosen as giving the finest fixation for work in spermatogenesis and while I have used a number of different fluids, I can add my testimony to the superiority of the

preparations when the tissues have been treated with one or the other of these two solutions. In order to check as far as possible any changes in the cells which might take place after the death of the animal the spiders were decapitated and the testes rapidly dissected out while the visceral mass was immersed in the fixing fluid. The paired, slightly convoluted tubular organs lie embedded in the liver and contain no pigment so that in immature spiders it is not always an easy matter to distinguish them from the spinning glands which lie ventral to them. As in many other forms, a cross section of the spider testis shows a more or less complete series of developmental stages, with the spermatogonia at the periphery and the cells gradually increasing in maturity toward the lumen. In the breeding season the lumen of the tube is found to be full of mature spermatozoa. Ripe spermatozoa were also taken from the pedipals and studied in smear preparations, sometimes stained *intra vitam* and sometimes fixed, before staining, by heating at the boiling point. Of staining methods, Heidenhain's iron-hæmatoxylin and Hermann's triple stain yielded the finest results.

The Spermatogonia.

The only comparatively recent work upon spider spermatogenesis of which I have any knowledge is that of J. Wagner. Unfortuately his paper is not accessible to me, but from his preliminary report and from several full reviews, I have been able to learn enough of his results to know that they differ widely from mine. He mentions the fact that the spermatogonia are larger than the spermatocytes even at the close of the growth period of the latter. This is true of the spermatogonia of the last generation, but in the early generations the cells are smaller. During the rest stage, when the chromosomes become granular and the chromatin granules are distributed along the linin reticulum, two chromosomes are conspicuous because they take no part in this disintegration (Pl. I., Fig. 1). From this point to the formation of the spermatozoön these two chromosomes can be identified by their shape, by their peripheral position and by the fact that they show a strong affinity for safranin, in the Hermann's staining method, while the other chromosomes take the gentian

violet excepting in the metaphase and anaphase, when they also take the safranin. By some authors this is supposed to be due to the presence of a greater amount of nucleinic acid at the height of the mitotic division and since the two peculiar chromosomes in the spider show this reaction constantly throughout the maturation processes it seems possible that they are more richly supplied with nucleinic acid than the other chromosomes. This is of special interest when we recall that the nuclei of spermatozoa contain a maximum of phosphorus.

The rod-shaped chromosomes are so numerous that it is difficult to make an accurate estimate of their number but by repeatedly counting those found in a cross section of the equatorial plate I believe the number to be forty (Pl. I., Fig. 2). In such a polar view of the equatorial plate two of the forty chromosomes are found in a peripheral position, thus reducing the number of other chromosomes to thirty-eight. The ordinary mitotic division occurs in which forty daughter chromosomes are carried to each pole, so it is puzzling to know why Wagner should say "Die Kerne der spermatogonien theilen sich nicht nach dem gewöhnlichen schema der Karyokinese aber auch nicht amitotisch." During mitosis the two peripheral chromosomes split longitudinally and are equally distributed to the two poles, just like the other chromosomes (Pl. I., Figs. 3, 4 and 5). During the telophase when the daughter chromosomes become granular and begin to spread out on the linin reticulum — even at the beginning of this disintegration — two are conspicuous because they remain unchanged and in the rest stage these two rods are sharply defined as they lie in the chromatin reticulum. Usually they lie side by side but are sometimes found at a short distance from one another and I am inclined to think that in the latter case they are slightly dislodged by the microtome knife and so become separated (Pl. I., Figs. 6, 7 and 8.)

A word might be said here in regard to the name of the peculiar chromosomes. In a recent paper ('04) Montgomery has suggested the general term heterochromosome to include the nuclear elements which have been described under various names, and he then divides them into two groups, according to their origin, as follows: (1) "The accessory chromosome"

(McClung), unpaired in the spermatogonia, as found in the Orthoptera. This would include the "chromosome spécial," described by de Sinéty; (2) the "chromatin nucleoli" (Montgomery), paired in the spermatogonia as found in *Euchistus*. This would include the "small chromosome" of Anasa, described by Paulmier. Such a classification does not apply in the spider, where the heterochromosomes are similar in appearance and behavior to those described by McClung as accessory chromosomes, but differ from them in arising as a double element. Sutton's work on *Brachystola* plainly shows the accessory chromosome to arise as a single element in the spermatogonia. The heterochromosomes of the spider, so far as their double origin is concerned, resemble the chromatin nucleoli of *Euchistus* and the "small chromosomes" of *Anasa*, but are otherwise different from them. In view of these facts, McClung's term is employed in this paper, and as the accessory chromosomes never fuse together, but only lie in close contact, the term will be used in the plural.

Primary and Secondary Spermatocytes.

Early in the prophase of the primary spermatocyte the chromatin is finely distributed on a delicate linin reticulum and the accessory chromosomes retain their individuality (Pl. I., Fig. 9). This stage I believe to be comparable to the synapsis, for at this time, or possibly earlier, the pseudo-reduction occurs. In none of my best preparations do I find a massing of the chromatin at one side of the nuclear cavity. Such a massing is found in poorly fixed material, but even then it occurs only in the later spireme stages. In his paper on *Peripatus* Montgomery has asserted that in synapsis is accomplished an end-to-end union, in pairs, of entire chromosomes, and that this numerical reduction occurs during the retrogressive stages of the telophase of the last spermatogonic division. Blackman, in his work upon Myriapods, in discussing this point, adds: "It can be stated with the greatest certainty that pseudo-reduction occurs during the telophase of the last spermatogonium and is completed before the reconstruction of the nuclear membrane." From the synapsis stage, represented in Fig. 9, arises the spireme. Like other workers, I find it impossible to state positively that it is segmented from the first

but I think such to be the case, and also that the nineteen loops are connected by a band of linin only. These loops grow thicker and show a longitudinal split gradually increasing in width, while the nucleus becomes more swollen with nuclear sap (Pl. I., Figs. 10–13). At this time a definite polarity can be noted, the blind ends of the loops being directed away from that portion of the cell which contains the greater mass of cytoplasm and the centrosome. The accessory chromosomes lie in the embrace of the free ends of a loop and near the centrosome. In testes nearing maturity, the majority of the cells are in this stage. This is followed by a rather rapid shortening of the loops when they draw down toward what Montgomery has called the distal pole (Pl. I., Figs. 14, 15). In his description of this stage Wagner says: "Der Linin faden (resp. die Reihen der chromatin-körner) bildet Schleifen, die alle gleich lang sind und die gleich Richtung haben: in dieser Weise theilt sich der Linin faden in Stücke von gleichen Länge. Gleichzeitig bildet sich der Nucleolus." While I agree with him in regard to the same general direction of the loops I do not agree with him in his statement that they are equal in length. At this stage the difference in the size of the loops can be plainly seen. This condition favors Montgomery's view of the end-to-end conjugation of chromosomes of like size during synapsis and which has been confirmed by Sutton in his work on *Brachystola*. It seems highly probable, in the light of recent research, that Montgomery's theory in regard to the pairing of paternal and maternal chromosomes during synapsis is the true explanation of the numerical reduction occurring at this time.

In the prophase of the primary spermatocytes, the bend of the loops becomes more acute, while the arms shorten and thicken and the now V-shaped chromosomes, varying in size, are scattered through the nuclear cavity. In doubly-stained material the accessory chromosomes appear as two red rods lying side by side among the violet V-shaped chromosomes. The latter now split from apex to base, opening out to form double V's and, sometimes after, sometimes during this process are drawn into the equator of the first maturation spindle (Pl. I., Figs. 16–20). In the metaphase the accessory chromosomes always take a per-

ipheral position, are connected by linin fibers to one pole only, and are drawn to this pole before the daughter V-shaped chromosomes are more than half way to their destination (Pl. I., Figs. 23, 24).

According to Wagner — "bei der ersten spermatocytentheilung theilt sich der Nucleolus entweder in der Ebene der Äquatorialplatte mit den Chromosomen zusammen oder auszerhalb denselben neben einem der spindelpole." In the latter case he believes it to be cast out into the cytoplasm. Here, as elsewhere, what he considers to be a "Nucleolus" is without doubt the pair of accessory chromosomes which often lie closely apposed to one another and arrive at one pole before the other chromosomes. Their eccentricity of position might mislead one into thinking that they are being thrown out of the nucleus.

In every case where a section is found cutting through the equatorial plate of the primary spermatocytic monaster transversely, cross-sections are found of the nineteen double V-shaped chromosomes and frequently are found also the accessory chromosomes which appear larger because of their oblique position in relation to the spindle axis. Their nearness to the cell-wall is here quite clearly demonstrated (Pl. I., Figs. 21, 22). During the telophase the nineteen V-shaped chromosomes enter into a partial rest, becoming granular but not forming a reticulum, while the accessory chromosomes in one of every two daughter nuclei stand out in a striking manner as two densely stained rods against the granular background and in sections stained with Hermann's method, their affinity for the safranin at a time when the other chromosomes take the gentian violet, makes them still more prominent (Pl. I., Fig. 25).

The nuclear membrane now forms, one nucleus containing a pair of accessory chromosomes, the other none (Pl. I., Fig. 26), and the V-shaped daughter chromosomes, attached by their apices are quickly drawn into the equator of the spindle for the second maturation division (Pl. I., Fig. 27). Frequently the cell body of the primary spermatocyte does not undergo division until toward the close of the telophase of the second maturation division.

Sequence of Reduction and Equational Divisions.

Most authors now grant that one transverse and one longitudinal division obtain in the maturation divisions of the germ cells, but there is still a lack of argreement in regard to the sequence of these two divisions. There has been a decided majority in favor of the view that the longitudinal division occurs first. Montgomery has emphasized the importance of determining the origin of the chromosomes in order to get at the truth of this matter and he claims to have established the fact that "the heterotypic mitosis, the first maturation mitosis, is not an equation division but separates entire univalent chromosomes, while the second maturation mitosis is equational." This conclusion is supported by the work of Korschelt on the ovogenesis of an annelid, by the work of Henking and Paulmier on Hemiptera, fo Miss Nichols on isopods and by several others. There is the

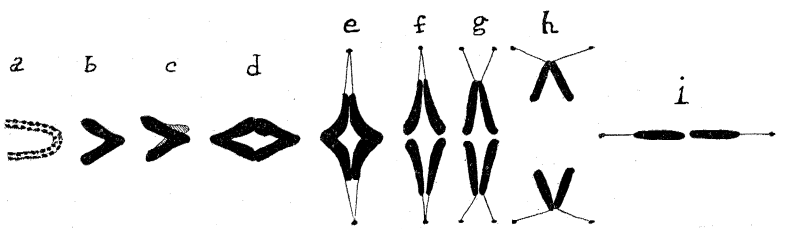

Fig. 1

possibility that uniformity in regard to the sequence of the divisions does not exist since in either case the ultimate result is the same, but if there is uniformity the spider spermatogenesis seems to me an especially good field for determining this point and it shows strong grounds for believing that the first division is a reduction division. The process is as follows: When pseudo-reduction occurs in synapsis, giving rise to nineteen loops of different lengths, there is at first no split visible in the thread of the loop. When the split does appear it becomes steadily more noticeable during the growth period and is then obscured in the condensation of the chromatin to form the thickened V-shaped chromosomes (text figure, *a* and *b*). In the prophase of the primary spermatocyte, the V's split from apex to base, parting along the line, I maintain, of the original, longitudinal split of

the loops in the spireme (*a* and *c*), and then open out into double V's (*d*). In the metaphase these double V's are so placed at the equator of the spindle that the longitudidal split is parallel to the spindle axis. This can be determined with certainty since often the splitting occurs after the chromosomes have taken up their position in the equatorial plane and can be seen at different stages of the process, the line of the split being always parallel to the spindle axis (Pl. I., Figs. 18, 19, and text figure, *e*).

Double spindle fibers connect the ends of the double V-shaped chromosomes with the centrosomes. To express it in another way, — after a V-shaped chromosome has become a double V by a split passing longitudinally along each arm, each half of each arm is connected by one linin fiber with the centrosome, but since the distal ends of every such pair are in close juxtaposition, we have the appearance of double spindle fibers passing from them to the poles. The first maturation division then takes place through what corresponds to the apex of the original V's and is a transverse or reduction division (*f*). When the centrosomes divide to form the daughter centrosomes for the second maturation spindle, one of each pair of linin fibers remains attached to one of the daughter centrosomes. When the latter have moved in opposite directions and have taken up their positions at right angles to the position of the mother centrosome (thus becoming the poles of the second maturation spindle) the V-shaped daughter chromosomes, formed from the longitudinal splitting of a single arm, are left attached by their apices in the equator of the spindle. The space between the arms of these single V's corresponds to the space between the halves of the longitudinally split spireme and, therefore, when the arms of the V are drawn to opposite poles, we plainly have an equational division (*g*, *h*, *i*).

To sum up: The first division occurs at a point corresponding to the bend of the loop in the spireme while the second occurs along the line of the original, longitudinal split of the spireme. Such an interpretation must surely be the true one if it be granted that the loops arise in the synapsis by a conjugation, end to end, of like chromosomes. And, even if the loops are supposed to originate by the spireme simply breaking up into the reduced number of chromosomes, still the sequence of the divisions would be as given above.

Significance of the Accessory Chromosome.

Considerable attention has been paid to the distribution of accessory chromosomes to the spermatids because opinions have differed in regard to it. Nothing could be clearer than the fact that, in the spider, during the first maturation mitosis, the two accessory chromosomes pass bodily over into one of the two daughter cells. In the second maturation mitosis the question is far more difficult to answer, partly because but one half of the cells contain the accessory chromosomes anyhow and partly because the V-shaped chromosomes attached to the equator of the spindle by their apices, cause a branching in the equatorial plate and thus the monaster is a much less clear subject for study than is found in the first spermatocytic monaster. A number of favorable cases were found, however, in which the two accessory chromosomes pass to but one pole and such cases, together with a careful study of the spermatids, have convinced me that not only in the first division, but also in the second the accessory chromosomes pass to but one pole, and are therefore, distributed to only *one fourth* of the spermatids (Pl. I., Fig. 28). In this respect my results differ from all other workers yet heard from. Henking and Paulmier found the hetero-chromosomes dividing in the first spermatocytic division, but passing undivided to one daughter cell in the second; McClung, Sutton and Blackman hold just the reverse. They find them taking no part in the first but dividing in the second division. In either of the above cases the result would be the same, *i. e.*, one half of the spermatids would contain no heterochromosomes, while the other half would contain them and could be called what Henking has styled "bevorzugten Tochterzellen." Montgomery finds the heterochromosomes dividing like the ordinary chromosomes in both divisions and they are, therefore, present in all of the spermatids, while in the spider they seem to stand aloof in both of the maturation mitoses and are, therefore, distributed to but one fourth of the spermatids.

In consideration of our limited knowledge in regard to the heterochromosome, and of the fact that nothing is known as to what part this peculiar nuclear element plays in fertilization, it is perhaps premature to say anything in regard to its significance.

McClung has suggested that the heterochromosomes might be sex-determinants and he is supported in this view by Sutton, Blackman and others. Paulmier regarded them as degenerating chromatin. Montgomery agreed with him in this and considers that they are "chromosomes that are in the process of disappearance, in the evolution of a higher to a lower chromosomal number." If only one fourth of the spermatids contain the heterochromosomes, as in the spider, they can scarcely be sex-determinants. Neither do they here show the characteristics of degenerating chromatin. That they represent some form of specialized chromatin, I cannot doubt, but that they are specialized for some metabolic function and comparable to nucleoli, as has been suggested by Montgomery, does not seem to me probable in view of the facts. I, therefore, venture to offer a fourth theory in regard to the function of the accessory chromosomes in the spider.

The breeding season of *Agalena nævia* comes late in the summer, the eggs being laid in August and September. While examining preparations made late in September I noticed a great many degenerating cells side by side with the ripe spermatozoa found in abundance in the lumen of the testis and in the ducts (Pl. II., Fig. 49). These cells are without nuclei and many of them are fragmented. My first conclusion was that the presence of so many fragmenting cells was due to the lateness of the season but on examination of sections prepared early in August a few cells undergoing degenerative processes were found even though but few spermatozoa had yet reached maturity. Sections made from the testis of *Pholcus phalangiodes* at the very height of the breeding season, in July, were most convincing. In *Pholcus* the spermatozoa are much more elongated than in any other species of spider examined (Pl. II., Fig. 51), but when mature they curl up as the others do. In the lumen and ducts were found hundreds of spermatozoa thus coiled up but a far greater number of round cells with rounded nuclei in which the linin and chromatin are no longer distinguishable. These cells vary in size — some as large as the germ cells, some very minute and in every way they resemble cells in the process of degeneration (Pl. II., Fig. 50, *d*). Further study showed that as a rule the degeneration does not begin until after the spermatozoa have

been emptied from the cysts into the lumen. The process then goes on very rapidly. Probably the degenerating cells of *Pholcus*, if examined near the close of the breeding season would be found to have lost their nuclei like those of *Agalena nævia*. It was not found possible to make an accurate count of the two kinds of cells in the ducts and hence it was not possible to determine with certainty their relative numbers but it was estimated that there were about three times as many of the degenerating cells as of the normal, ripe spermatozoa. What could be the determining cause? It will be remembered that there are three times as many spermatozoa without the accessory chromosomes as with them, and it occured to me that possibly only one fourth of the spermatids, the "bevorzugten zellen," become functional spermatozoa. Platner and O. Hertwig have shown that the two divisions which form the polar bodies of the egg are homologous to the last two divisions of male germ cells but that while in the female germ cell the products of division are very unequal in size and only one of the four is functional, in the male germ cell they are equal in size and each of the four is functional. If it can be proven that three fourths of the sperm cells are aborted, just as three fourths of the ova are, the parallelism in the spermatogenesis and ovogenesis will be found to be even more complete than has hitherto been supposed. There are at least *a priori* reasons for believing such to be the case and I was still further strengthened in this position when my attention was called to a short paper by Meves in which he describes the finding of "polar bodies" in the testis of the honey bee and other Hymenoptera. "Die Spermatocyten 1. Ordnung bei den genannten Hymenopteren stoszen ebenso wie sonst die Eier bezw. Ovocyten 1. Ordnung nach einander zwei "Richtungskörper" aus; von diesen besitzt jedoch nur der zweite einen Kern, während der erste ausschlieszlich von Cytoplasma gebildet wird . . . . Die ersten Richtungskörpen gehen nach einiger zeit zu Grunde. Die zweiten Richtungskörper dagegen beginnen ebenfalls sich zu Sprermien zu entwickeln, wobei ihre Kerne dieselben Veränderungen wie die Kerne der groszen zellen und zeitlich parallel mit ihnen durmachen-jedoch scheint dieser Entwickelungsprozesz schlieszlich, wenn auch erst sehr spät, zum Stillstand zu kommen und in Degeneration überzugehen."

We might here mention once more that the accessory chromosomes show a staining reaction throughout which the other chromosomes show at the height of mitosis and which some think to be due to the presence of a larger amount of nucleinic acid at that time. Now while staining reactions are not a safe criterion, they may give us at least a rough test of the chemical conditions in a cell, and since the nuclei of spermatozoa have been found to contain a maximum of nucleinic acid, and since the "bevorzugten zellen" in the spider might be richer in nucleinic acid, on account of the presence of the accessory chromosomes, than the remaining three fourths of the male germ cells which are not so favored, we might here see a new significance in the accessory chromosomes.

Spermatids and Spermatozoa.

A study of the spermatids will throw further light upon the subject of the distribution of the accessory chromosomes. In most cases it is evident that when the secondary spermatocytes, which do contain the accessory chromosomes, divide, the latter pass to but one of the resultant spermatids (Plate II., Figs. 29–33). Figs. 34 and 35 show spermatocytes which are not "favored cells." Sometimes each of the two spermatids resulting from the division of a favored spermatocyte seems to contain one accessory chromosome, but I think this should be regarded as an exceptional case (Pl. II., Fig. 37). At a later stage in the formation of the spermatozoön it is impossible to determine which cells contain the accessory chromosomes and which do not. At the beginning of the process of the condensation of the chromatin to form the head, the two accessory chromosomes become closely applied to one another, then appear to fuse together. They still take the safranin stain and form a center into which the chromatin reticulum which takes the violet stain, is gradually drawn until all of the chromatin forms a compact mass stained brilliant red. In the spermatids which lack the accessory chromosomes the chromatin at one point in the reticulum forms a net-knot which now takes the safranin stain and it becomes the center of condensation and so simulates the appearance of the favored cells. At such a stage one might be mislead into think-

ing that every spermatid contains the accessory chromosomes. This stage in *Agalena* is shown in Fig. 38 and in *Epeira*, Figs. 42–44. In all cases the chromatin assumes a crescentic form, the anterior end bends in, the posterior end folds over it and we see the mature spermatozoa each consisting of a crescent-shaped nucleus, covered by a pellicle of cytoplasm and curled up. In this condition they are found in abundance in the lumen of the testis, in the ducts and in the pedipalps (Figs. 39–41).

In Fig. 48 is pictured a spider spermatozoön after Wagner in which he demonstrates a tail. This is of special interest to me because I have not succeeded in finding an organ of locomotion in connection with the spermatozoön. As he also worked upon *Agalena*, I am surprised to find my results so different from his. He claims that "Die Spermatozoen haben auf gewissen Stadien bei allen Species einen typischen Schwanz mit Achsenfaden. Der Achsenfaden bildet sich im Protoplasma der Spermatocyte (resp. Spermatide) zuerst als ein kurzes Stäbchen welchem bisweilen einige Archoplasmakörnchen anliegen. Mit dem Kerne verbindet er sich erst nach dessen Umwandlung in die Chromatinplatte."

"Wo sich Achsenfaden und Chromatinplatte verbinden liegt am Rande der letzeren ein Zähnchen." In striving to get light upon these points I have studied the spermatozoa of about a dozen different species of spiders, have stained them *intra vitam*, have made smear preparations fixed by heating at the boiling point, have studied, with painstaking care, sections fixed and stained in a great variety of ways, and in no case has a tailed spermatozoön been found with the exception of *Pholcus* and even here the elongated portion which might be looked upon as a tail, stains more like a middle piece and its cytoplasmic origin is questionable (Fig. 51). My belief is that the "tail" which Wagner saw was nothing more nor less than the outline of a vesicle which is nearly always in evidence when the spermatid is being transformed into the spermatozoön, and that what he describes as a little tooth is really nothing more than the anterior end of the head bent under, although in this case there should be a rounded bend instead of what he figures (Figs. 46, 47). I would be glad to believe in the existence of a tail and have

earnestly tried to demonstrate it but so far the method of locomotion of the spider spermatozoön remains an unsolved mystery to me. In a future paper I hope to be able to give some light upon this subject as well as upon the rôle played by the accessory chromosomes in fertilization. As my work now leaves it, the functional spermatozoa would contain an uneven number of chromosomes — nineteen ordinary ones and two accessory chromosomes, and it is not clear how the somatic number of forty chromosomes is made up in the cleavage nucleus of the ovum unless it be found that accessory chromosomes are thrown off in the polar bodies, thus leaving the mature ovum with only nineteen chromosomes. These nineteen, added to the twenty-one brought in by the spermatozoön would make the total required; forty chromosomes.

Summary.

1. The spermatogonia contain two accessory chromosomes and thirty-eight other chromosomes.

2. In the primary spermatocytic division the two accessory chromosomes pass over undivided into one of the daughter cells. The reduced number of other chromosomes is nineteen and these divide transversely.

3. In the secondary spermatocytic division, the two accessory chromosomes again pass over undivided into one of the daughter cells. The nineteen other chromosomes divide longitudinally.

4. Only one fourth of the spermatozoa contain the accessory chromosomes.

5. Apparently the remaining three fourths of the spermatozoa degenerate after almost or altogether reaching maturity. In this respect they are regarded as homologous to the polar bodies thrown off by the ovum.

The University of Pennsylvania,
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Explanation of Figures.

All drawings were made at a magnification of about 2,000 diameters and then reduced one third. All figures were drawn from Agalena unless otherwise specified, and were drawn with the aid of the camera lucida.

Plate IX.

Fig. 1. Spermatogonium in resting stage.

Fig. 2. Pole view of equatorial plate of spermatogonic monaster.

Fig. 3. Spermatogonic monaster.

Figs. 4–5. Anaphase of spermatogonic monaster.

Fig. 6. Daughter cell of last spermatogonial division showing disintegration of the chromosomes.

Figs. 7–8. Resting cells.

Fig. 9. Formation of spireme, "synapsis."

Fig. 10. Completion of spireme.

Figs. 11–13. Coarse spireme with longitudinal split.

Figs. 14–15. Shortening and thickening of loops of segmented spireme.

of primary spermatocyte with loops transformed into V-shaped chromosomes.

Fig. 17. Splitting of chromosomes.

Figs. 18–20. Primary spermatocytic monaster.

Figs. 21–22. Sections of equatorial plate.

Fig. 23. Primary spermatocytic metaphase.

Fig. 24. Primary spermatocytic anaphase.

Fig. 25. Late anaphase or telophase.

26. Reconstruction of daughter nuclei.

Figs. 27–28. Secondary spermatocytic monaster.

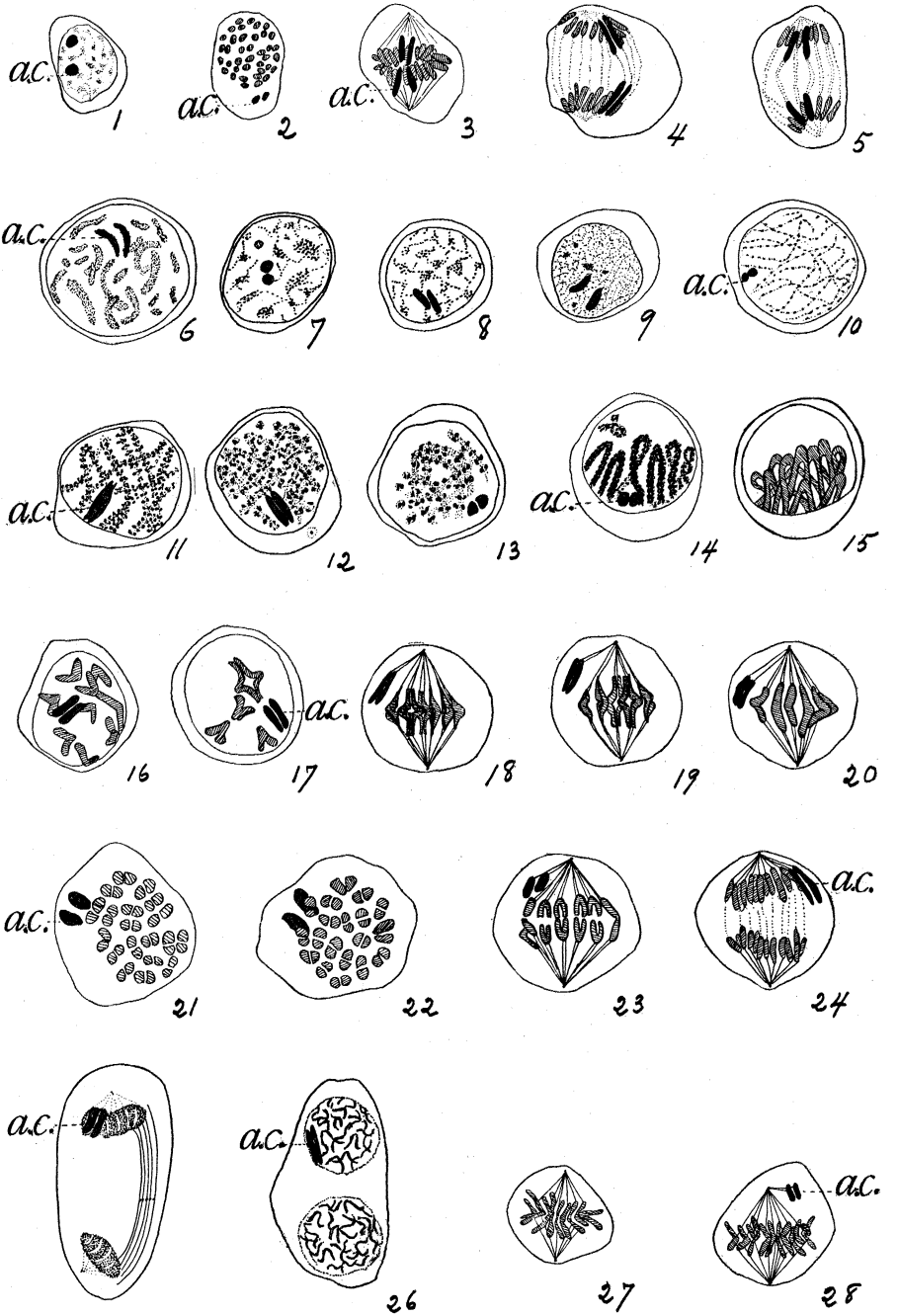

a.c.
1
a.c.
2
a.c.
3
4
5
a.c.
6
7
8
9
a.c.
10
a.c.
11
12
13
a.c.
14
15
16
a.c.
17
18
19
20
a.c.
21
22
23
a.c.
24
a.c.
a.c.
26
27
a.c.
28

PLATE X.

FIGS. 29–39. Spermatids.

FIGS. 40, 41, 46, 47. Spermatozoa.

FIGS. 42–45. Spermatids of *Epeira sclopetaria*.

FIG. 48. Spermatozoön of *Agalena*, nach Wagner.

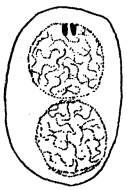
FIG. 49. Normal spermatozoa and degenerating cells. *Agalena*.

FIG. 50. Normal spermatozoa and degenerating cells. *Pholcus*.

FIG. 51. Spermatozoa of *Pholcus phalangiodes*.

ABBREVIATIONS.

a.c., accessory chromosomes; *sp.*, spermatozoön; *d.c.*, degenerating cells; *t.* tail of spermatozoön, nach Wagner; *v*, vesicle.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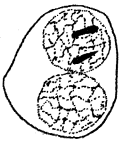
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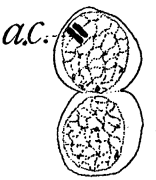

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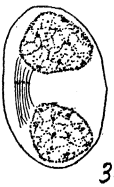
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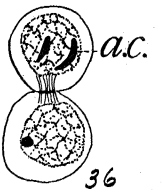

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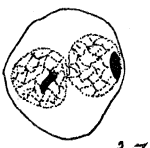
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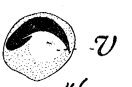

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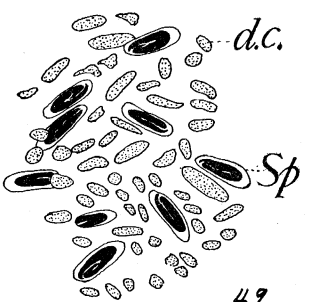

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